TUBER AND LEAF STRUCTURE OF *ONDINEA PURPUREA* DEN HARTOG (NYMPHAEACEAE)

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ABSTRACT

Ondinea is a monotypic hydrophytic genus endemic to non-perennial streams in the northern region of Western Australia. Tuber and leaf structure have been examined using light microscopy and scanning electron microscopy. The tubers are globose to oblong in shape and reddish brown to light golden brown in color. Tuber apices are densely covered with fine hairs. Dormant tubers are smooth in texture with protruding wart-like leaf, root and flower scars. Leaves and flowers occur as members of the same genetic spiral. Adventitious roots occur abaxially to the leaves. Floating and submerged leaves differ structurally. Floating leaf blades consist of a uniseriate epidermis with stomata restricted to the upper surface, netted veins, and mesophyll with palisade parenchyma, spongy parenchyma, and astrosclereids. Submerged leaf blades are thinner, lack stomata, and the mesophyll lacks differentiation.

INTRODUCTION

Ondinea purpurea den Hartog is a monotypic hydrophytic genus endemic to Western Australia. Two subspecies are currently recognized: *Ondinea purpurea* subspecies *purpurea* and *O. purpurea* subspecies *petaloidea* Kenneally and Schneider.

Ondinea is restricted in distribution to non-perennial streams overlying sandstone formations in the northern Kimberley region of Western Australia. Collection sites of the plant include the Prince Regent River system, tributaries of the Mitchell River, streams near Kalumburu Mission, a freshwater creek flowing into Pauline Bay and Woppinbie Creek (den Hartog 1970; Hnatiuk and Kenneally 1981; Kenneally and Schneider 1983; Schneider 1983; Forbes, Kenneally, and Aldrick 1988). *Ondinea purpurea* subsp. *petaloidea* is currently known only from the Mitchell River system (Kenneally and Schneider 1983; Schneider 1983).

The growing season of the plant occurs during northern Australia's summer wet season extending from December to April. During this time the plant grows in clear, frequently rapidly moving water. The streams flow from December to April, becoming dry by June (Beard 1976). The plant survives the dry winter season as dormant tubers buried in the alluvial sand of the stream beds.

Den Hartog (1970) formally described the species, provided the binomial and, based on morphological similarities to *Nymphaea*, classified *Ondinea* within the Nymphaeaceae. Den Hartog (1970) considered *Ondinea* closely related to *Nymphaea* and stated that "In general the *Ondinea* flower can be regarded as an apetalous *Nymphaea* flower". He viewed *Ondinea* as also differing in the absence of an aril, carpellary appendages, a stigmatic cup, and in the presence of a greatly elongated floral axis. Muller (1970) described the pollen of *Ondinea* and found it very similar to that of *Nymphaea* providing additional evidence of a close relationship between the two taxa. Studies of seed structure and morphology (Schneider and Ford 1978; Collinson 1980), floral morphology (Kenneally and

Schneider 1983; Schneider 1983), reproductive biology (Schneider 1983; Schneider, Moseley, and Williamson 1983), and the discovery of a petalliferous subspecies (Kenneally and Schneider 1983), have provided additional evidence indicating a close relationship between *Nymphaea* and *Ondinea*, thus supporting the taxon's placement in the Nymphaeaceae.

This paper examines tuber morphology and leaf structure of *Ondinea purpurea*. The investigation expands our knowledge of *Ondinea* and provides new systematic evidence with which to interpret phylogenetic relationships among the genera included in the Nymphaeaceae.

MATERIALS AND METHODS

Tubers of subsp. *petaloidea* used for morphological examinations were collected from tributaries (14°41′40″S, 125°40′30″E) of the Mitchell River on July 8, 1988. Tubers prepared for anatomical observations were collected from the same site in January, 1982 during the growing season of the plant. Tubers of subsp. *purpurea* used to examine morphological features were collected July 9, 1988 from Gutter Creek, the third creek approximately 7 km west of Kalumburu Mission along the road to the ocean. Tubers and submerged leaves of subsp. *purpurea* utilized for anatomical observations were collected in January 1982 from a small unnamed tributary to Camp Creek, near the Camp Creek gauging station (14°54′S, 125°44′E). Floating leaves of subsp. *purpurea* were collected in January 1982 near Kalumburu Mission from the type habitat noted by W. Leutert (den Hartog 1970). Voucher specimens of both subspecies are housed in the Southwest Texas State University Herbarium (SWT) and the Western Australian Herbarium (PERTH).

Tubers and leaves prepared for light microscopy were fixed in formalin-acetic-alcohol (Johansen 1940). Light microscope slides were prepared following standard microtechnical procedures. Following fixation, the material was washed then dehydrated with 2,2-di-methoxypropane (Postek and Tucker 1976). The material was then infiltrated with and embedded in paraplast-plus (Johansen 1940) and sectioned at 7-10 microns using a Spencer "820" rotary microtome. Sections were stained using a combination of Harris' haematoxylin, safranin, and fast green (Johansen 1940). The sections were examined using a Spencer A0 light microscope. Line drawings of the sectioned material were prepared freehand. Macrophotography was accomplished using a light tray, which provided a source of bottom illumination, and incandescent lighting from above. Photographs were taken using a Nikon 35 mm camera with Kodak plus X pan film (ASA 125). Standard deviations are expressed parenthetically for numerical counts of leaf anatomical features.

Tubers examined with a scanning electron microscope (SEM) were dehydrated in an ethanol series over a period of 7 days, mounted on SEM studs using graphite paint, and coated with a layer of gold in a Denton vacuum sputter-coating unit. Samples were observed and photographed with a Cambridge 90-B scanning electron microscope at 10 KeV. Photographs were taken using Polaroid 55 positive/negative film.

OBSERVATIONS

Habit and Habitat

The tubers of subsp. *petaloidea* were excavated from dry and from still moist stream beds. Tubers were found at depths of 5-26 cm in sandy-humus

soils. Abundant seedlings similar to those described by Kenneally and Schneider (1983) were observed in remaining pools of water. The seedlings were found to form small light brown primary tubers c. 2-3 mm in diameter with strap-shaped leaves and adventitious roots. A few plants bearing mature submerged leaves with undulate leaf margins were also present.

The tubers of subsp. *purpurea* were typically found at depths of 15-23 cm in wet sandy-humus soil. Gutter Creek also contained pockets of stagnant water in which numerous seedlings, similar to those of subsp. *petaloidea*, were observed. Dry, black mature leaves were observed on the moist sandy stream banks.

Tuber Morphology

The tubers of O. *purpurea* are globose, conical, or oblong in shape. Globose tubers are typically reddish brown in color, while oblong tubers tend to be light golden brown. The majority of subsp. *purpurea* tubers are globose to conical, a few are somewhat oblong but not to the extent of subsp. *petaloidea* tubers (Figure 1).

Tubers of subsp. *petaloidea* are typically larger in size than tubers of subsp. *purpurea*. A sample of 60 subsp. *purpurea* tubers was measured and found to vary in size from 0.8 cm in length x 0.7 cm in width to 3.5 cm x 2.3 cm (Table 1; Figure 1, A-E). A sample of 100 subsp. *petaloidea* tubers was measured and the tubers found to vary in size with the smallest tuber 1.0 cm x 0.8 cm and the largest tuber 6.2 cm x 3.8 cm (Table 1; Figure 1, F-H).

Table 1. Comparison of average tuber dimensions between subspecies of *Ondinea*.

	Taxon		
	subsp. *purpurea* n = 60	subsp. *petaloidea* N = 100	Significance (p)
Length (cm)	1.84 ± 0.09	2.81 ± 0.12	< 0.0001
Width (cm)	1.23 ± 0.06	1.64 ± 0.02	< 0.0001

± values represent Standard Error of the Mean. Probability calculated using standard two-tailed Student *t* test.

Vertical alignments of 3-6 tubers, with the largest, oldest tuber at the base and successively smaller, younger tubers formed above the older ones, were commonly observed. This feature was also observed by Leutert (den Hartog 1970) and Schneider (1983).

The tuber apices are densely covered with fine, light brownish hairs that conceal the apex, young developing leaves and flower buds (Figure 1, I). The tubers are covered by a smooth periderm with protruding, wart-like leaf, root, and flower scars comparable to those described for *Nymphaea* (Conard 1905). Some tubers possess only a few scars, while others are extremely warty due to the presence of abundant scars.

Observation of the scars reveals that the leaves and flowers are arranged in a helical phyllotaxy (Figure 1, I). The flowers are extra-axillary and are produced as members of the genetic spiral, occupying leaf sites in the parastichies. Adventitious roots occur abaxially to the leaves. One or two roots occur beneath each leaf. Where two roots are present, they occur one beneath the other typically 0.5-1 mm apart (Figure 1, I).

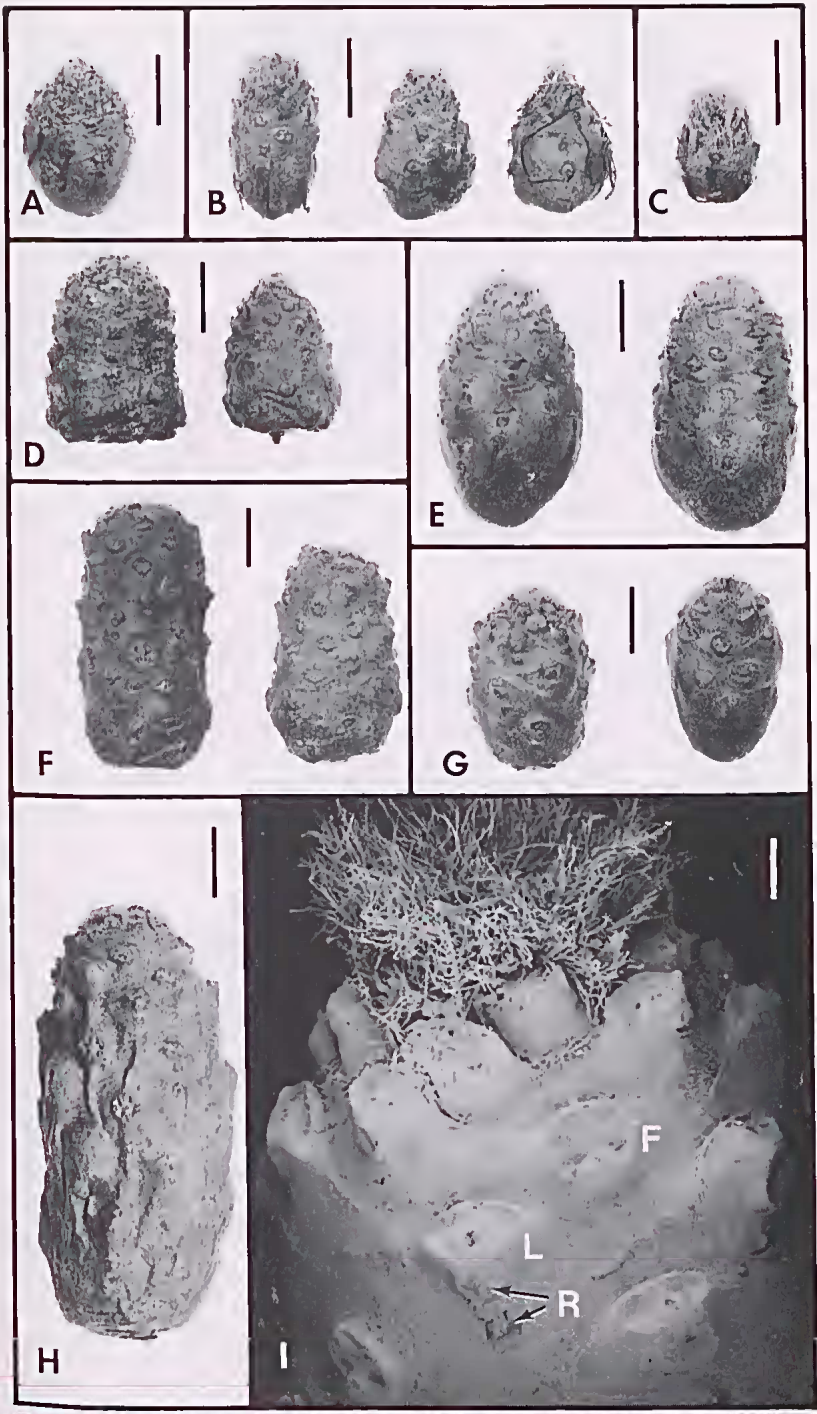

Figure 1. Macrophotographs of the tubers of *Ondinea purpurea* subsp. *purpurea* (A-E) and *Ondinea purpurea* subsp. *petaloidea* (F-H). I — Scanning electron micrograph of the tuber of *Ondinea purpurea* subsp. *purpurea* showing flower peduncle scars (F), leaf petiole scars (L), root scars (R), and hairs covering the apex. Bars = 1 mm.

The petiole scars are subtriangular in shape and 2-3 mm wide. One (typical of subsp. *purpurea*) or two (typical of subsp. *petaloidea*) central vascular bundle scars are apparent. When two are present, the lower of the two is larger. A depression occurs laterally to each side of the central bundle scars. These depressions represent the two largest air canals of the petiole.

The root scars are circular and c. 0.5-1 mm in diameter. Where two root scars occur, the lower is often larger and typically projects downward. The downward projection is often extreme and it is likely that these are remains of abscised contractile roots.

The peduncle scars are circular and flush with or slightly elevated above the surface of the tuber. The scars are c. 1.5-5 mm in diameter. Vascular bundle scars occur along the periphery of the peduncle scar centrifugal to and alternating with depressions representing large air canals. There are typically 4-5 bundle scars and 4-5 air canals in the peduncles of subsp. *petaloidea*. This subspecies usually has an additional vascular bundle scar occupying the center of the peduncle. The peduncles of subsp. *purpurea* typically have 3-4 bundle scars and 3-4 air canals, and lack a central bundle scar. Structurally the peduncles consist of a uniseriate epidermis with hydropotes, angular collenchyma, aerenchyma, crystalliferous astrosclereids, air canals ranging from 0.01 to 0.95 mm in diameter, and two systems of vascular bundles (Williamson and Moseley, pers. observations).

Leaf Structure

The leaf morphology of subsp. *purpurea* was described by den Hartog (1970) and Kenneally and Schneider (1983). Juvenile floating leaf blades are narrow ovate with entire, slightly undulate margins. Mature floating leaf blades, as described by den Hartog (1970) were not observed. The juvenile leaf blades are c. 7 cm long and 2 cm wide (Figure 2, A). Submerged leaf blades are 10-17 cm long, deeply cordate with entire strikingly undulate margins (Figure 2, C). Leaf petioles are c. 10-40 cm long.

Structurally the leaves consist of a uniseriate epidermis, ground tissue, and vascular bundles. Non-branched articulated laticifers occur scattered throughout the leaf ground tissue and are associated with the veins where they typically occur directly centrifugal to the primary phloem.

The epidermes of floating leaf blades are composed of ordinary epidermal cells, uniseriate trichomes (referred to as hydropotes), and stomata. The ordinary epidermal cells are square to rectangular in shape with nearly straight or slightly wavy outlines. There is a cuticle and some cutinization of the outer tangential walls. The cuticle is exceedingly thin on the lower epidermal surface compared to the upper surface. Stomata were observed only in the upper epidermis. The guard cells are c. 0.02 mm long and 0.01 mm wide and kidney-shaped. A flange of wall material occurs on the outer surface of each guard cell. The stomata are scattered throughout the adaxial epidermis. Generally the stomata are separated by 2-3 ordinary epidermal cells. Subsidiary cells are lacking and the stomatal complexes are anomocytic. The average number of stomata observed was 100($\pm$14) per mm^2. Hydropotes are abundant components of the lower epidermis and are occasionally present in the upper epidermis. The average number of hydropotes observed in the abaxial surface was 145($\pm$23) per mm^2. Each hydropote consists of 2-3 lenticular cells, with the distal cell enlarged, dome-shaped, and often filled with a darkly staining substance that may be tanniniferous. A thin cuticle covers the hydropotes. Gessner (1956) observed minute pseudoperforations in the hydropote cuticle of other

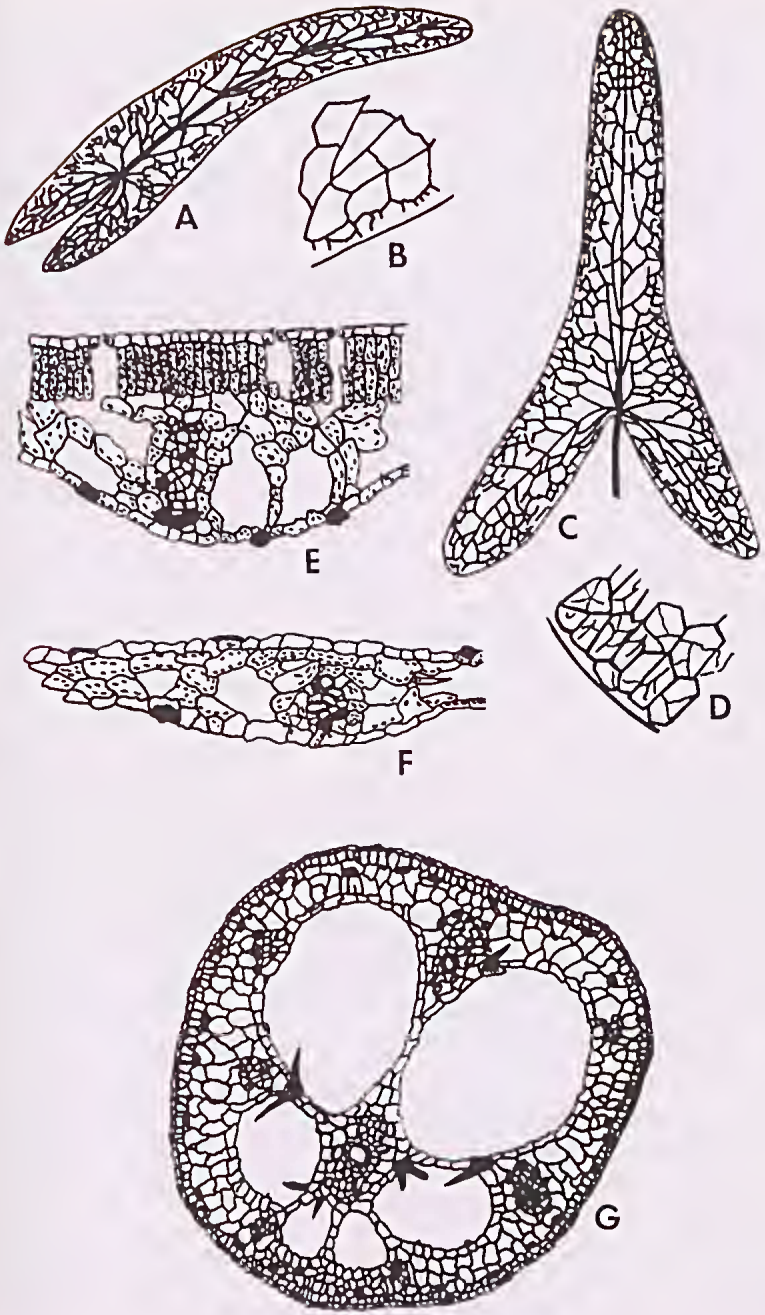

Figure 2. Line drawings of the leaves of *Ondinea purpurea* subsp. *purpurea*. A — Juvenile floating leaf blade 0.45X; B — marginal ultimate venation of the floating leaf blade 200X; C — submerged leaf shown without undulating margins 0.50X; D — marginal ultimate venation of the submerged leaf blade 200X; E — cross section of the floating leaf blade illustrating well differentiated mesophyll 130X; F — cross section of the submerged leaf blade 70X; G — cross section of the floating leaf petiole illustrating symmetrical arrangement of air canals and vascular bundles 60X.

water lilies. Functions ascribed to hydropotes include water intake (Mayer 1914; Lüttge 1964) and transpiration in emergent leaves (Gessner 1956; Bukowiecki and Furmanowa 1964; Goleniewska-Furmanowa 1970). Hydropotes were the only type of trichome observed in the epidermis.

The mesophyll of the floating leaf blade (Figure 2, E) consists of palisade parenchyma, spongy parenchyma and sclereids. Palisade parenchyma, 1-3 cell layers in depth, occurs directly beneath the upper epidermis. Large substomatal chambers extend through the palisade parenchyma. Approximately half the leaf blade is occupied by palisade parenchyma, with the remainder of the mesophyll consisting of spongy parenchyma. Sclereids occur in both regions of the mesophyll. Some sclereids were observed to extend from the upper to lower epidermis. The sclereids range in shape from bipolar to highly branched astrosclereids. The arms of the sclereids typically project into large air canals and intercellular spaces. Calcium oxalate crystals occur embedded in the sclereid walls. The vascular bundles are collateral and normally oriented. Venation is actinodromous (Figure 2, A and C). Marginal ultimate venation is looped and the veinlets are branched (Figure 2, B and D) based on Hickey's (1979) classification of dicotyledonous leaf architecture. The midrib region protrudes c. 0.5 mm below the remainder of the lower epidermal surface. A narrow band of angular collenchyma, c. 2 cell layers thick, occurs just centripetal to the abaxial epidermis in the midrib. The midvein is surrounded by numerous air canals ranging from 0.04 to 0.35 mm in diameter. Floating leaf blades are c. 0.25 mm thick, except in the midrib region where the blades are c. 1.0 mm thick.

Submerged leaf blades of subsp. *purpurea* are thinner, c. one-half the thickness of a floating leaf blade. They are c. 0.1 mm thick except in the midrib region which is c. 0.5 mm thick and protrudes below the rest of the blade. The epidermis consists of ordinary epidermal cells and hydropotes which are distributed in both surfaces, with an average number of 40(±15) per mm^2. Neither stomata nor cuticle was observed. The ordinary epidermal cells are rectangular to polyhedral with slightly wavy margins. The mesophyll is not differentiated (Figure 2, F). Astrosclereids occur but are less abundant than in floating leaves. Venation and structure of the vascular bundles are similar to floating leaves, but differ in possessing reduced vascular tissue, less lignification of the tracheary elements, and absence of collenchyma in the midrib.

The petioles are c. 1-2.5 mm in diameter and circular in transection with a slightly flattened adaxial side. Ordinary epidermal cells and hydropotes compose the epidermis. The ground tissue consists of collenchyma, aerenchyma and astrosclereids. A well developed sheath of angular collenchyma, 2-3 cell layers thick, occurs directly inside the petiole epidermis in floating leaves. The collenchyma present in submerged petioles is not as extensive and the cell wall thickenings are not as well developed as in the petioles of floating leaves. Aerenchyma occurs centripetally to the collenchyma. Astrosclereids are abundant components of the arenchymatous regions. The density of astrosclereids is much less in submerged leaves than in floating leaves. The sclereids are most frequently distributed with the body in a partition and the arms projecting into the air canals. There are typically eight air canals separated by predominantly uniseriate partitions. The air canals are of four sizes ranging from 0.04 to 0.70 mm in diameter, with two canals of each size adjacent to each other, forming two rows of air canals near the centre of the petiole (Figure 2, G). Diaphragms, noted in the root air canals of *Ondinea* (den Hartog 1970)

have not been observed in the petiole air canals. Two large vascular bundles occur along the median plane of the petiole, centripetal to the air canals. The upper bundle is collateral and normally oriented. The lower one is a double bundle consisting of a protoxylary lacuna with conducting tissues to the inner and outer side. Smaller, normally oriented, collateral vascular bundles occur around the periphery of the petiole; 6 bundles occur in the petioles of floating leaves while only 2 were observed in submerged leaf petioles. The vascular bundles extend through the petiole in an essentially straight course.

The vascular bundles of the peduncles (Williamson and Moseley, pers. observations), tubers and leaves consist entirely of primary vascular tissue. The phloem is comprised of sieve-tube elements with transverse to nearly transverse end walls and simple sieve plates (Type III elements, Zahur, 1959), companion cells, and parenchyma cells. The xylem consists of annular, helical, and weakly reticulate tracheary elements and parenchyma cells. Tannins are common components of parenchyma cells in both xylem and phloem tissue.

DISCUSSION

This study has revealed several anatomical characters that support the placement of *Ondinea* within the Nymphaeaceae. Features described such as the presence of air canals, aerenchyma, limited supportive tissue and xylem tissue which is qualitatively and quantitatively reduced are known to commonly occur in aquatic plant species (Kaul 1976; Esau 1977) of very remote phylogenetic relationships and, therefore, are not useful in determining taxonomic affinities.

Studies of the leaf anatomy (Goleniewska-Furmanowa 1970), numerical taxonomy (Bukowiecki, Furmanowa, and Oledzka 1972) and foliar sclereids (Rao and Banerjee 1979) of the Nymphaeaceae have suggested several anatomical characters which are apparently restricted in occurrence to the taxon and therefore provide useful systematic evidence. The Nymphaeaceae characteristically possess foliar sclereids that are lacking in two closely related aquatic families, the Cabombaceae and Nelumbonaceae. Since the character is absent in these aquatic taxa it is likely that the feature is indicative of phylogenetic affinities rather than a reflection of ecological convergence. Other structural characters present in the Nymphaeaceae, yet absent in the Cabombaceae include laticifers and tanniniferous cells. The presence of these characters in the leaves of *Ondinea*, together with tuber morphology, suggest that the taxon is properly classified within the Nymphaeaceae close to *Nymphaea*.

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FROM FIELD AND STUDY

Another Record of the Rednecked Phalarope (*Phalaropus lobatus*) in South Western Australia — The last recorded observation of this northern hemisphere migrant comes from Rottnest Island. The bird was observed over several days by Smith and Saunders on February 4, 1980. It was reported in the Western Australian Naturalist Vol. 14/8.

On November 11, 1986 we carried out a routine bird count at Lake Hinds (30°47'S, 116°34'E). On the southern shore a stationary raft of numerous Banded Stilts could be seen. In front of that group of birds an unusually active wader was noticed busily paddling and circling around. While picking frequently at the water's surface, this activity was often interfered with by individual Stilts. The bird was much smaller than the latter.

Almost white with a black eyespot and stripe on an otherwise whitish face and chest. The back was grey with the wingcovers and primaries set off in dark grey. The short tail was slanted slightly upward. It was undoubtedly a Redneck Phalarope in eclipse plumage.

We returned to the lake one week later but were unable to sight it again.

— O. MUELLER, 7 Hamer Avenue, Wembley Downs, WA 6019